

## Inheritance of Growth Habit in Pigeonpea

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### ABSTRACT

Determinate (DT) pigeonpea [*Cajanus cajan* (L.) Millsp.] has a production advantage but the genetics of this trait and indeterminate (IDT) and semideterminate (SDT) growth habits are not well defined. Inheritance of DT, SDT, and IDT growth habits in short-duration pigeonpea was studied in  $F_1$ ,  $F_2$ , and  $BC_1F_1$  generations of 15 crosses involving six parents (two of each growth habit) grown in the field in 1986. The segregation pattern in the crosses involving IDT and DT parents indicates that IDT growth habit is governed by a single dominant allele. Similarly, crosses between SDT and DT parents showed that the SDT trait also is controlled by a single dominant allele. The  $F_2$  population of the crosses between IDT and SDT parents segregated in the ratio of 12 IDT to 3 SDT to 1 DT, suggesting that the expression of the SDT allele ( $Dt_2$ ) was masked by the presence of the IDT allele ( $Dt_1$ ) and that the homozygous recessive genotype for both genes ( $dt_1dt_1dt_2dt_2$ ) has the DT phenotype. The results obtained in  $BC_1F_1$  with both parents also supported the  $F_2$  data. The desirable determinate phenotype can be obtained from crosses of different phenotypes, including IDT  $\times$  SDT, provided the IDT parent has the  $Dt_1\_dt_2dt_2$  genotype.

PIGEONPEA possesses three distinct growth habits of plant types (Fig. 1): determinate, semideterminate, and indeterminate. In plants with DT growth habit, the inflorescence is short, the apical bud develops into the flower, the sequence of inflorescence production is basipetal (Sheldrake, 1984), and the flowers occur more or less in the same plane. In IDT plants, the inflorescence is large, with a vegetative apical bud resulting in continuous growth. The flowers occur in axillary racemes spread over a considerable length of the stem. The inflorescence in plants with the SDT growth habit, after initiation of reproductive growth, grows as in IDT plants, resulting in elongated flowering or fruiting branches terminating with a flower as in the plants with DT growth habit. Because of the short inflorescence, the pods in DT plants are borne in closely packed clusters, whereas in SDT and IDT plants the pod clusters are distributed on their elongated inflorescences. The short stature of the DT plant types makes them amenable to efficient crop management practices, such as foliar insecticide application and mechanized field production. Indeterminate plants, on the other hand, grow taller; hence, efficient management and mechanization become difficult. Most of the traditional medium (maturing in 150–200 d) and long-duration (maturing in >200 d) pigeonpea cultivars are tall indeterminates, resulting in low productivity, mainly because of inefficient pest (mainly *Helicoverpa armigera* pod borer) control.

Information on the genetics of growth habit in pigeonpea is limited and contradictory (Reddy and Rao, 1974; Waldia and Singh, 1987). To our knowledge,

only two studies have been reported on the inheritance of IDT growth habit in pigeonpea, and neither studied the SDT growth habit. Reddy and Rao (1974) reported that IDT is governed by a single dominant gene. Waldia and Singh (1987) suggested involvement of two dominant genes with inhibitory interaction of one of them to control the IDT growth habit. This paper presents additional data on the inheritance of IDT, SDT, and DT growth habit in short-duration pigeonpea.

### MATERIALS AND METHODS

Six short-duration (maturing in <140 d) pigeonpea advanced lines (two of each growth habit) developed by a pedigree method of breeding from crosses involving a short-duration cultivar and a medium- to long-duration landrace, were selected as parents. Lines selected included ICPL 83008 (DT), 83024 (DT), 269 (SDT), 83032 (SDT), 143 (IDT) and 161 (IDT). These are adapted lines with good agronomic performance. Lines ICPL 269 and 83008 were developed from the cross 'UPAS 120'  $\times$  ICP 7035, whereas lines ICPL 83024 and 83032 were developed from the cross 'Prabhat'  $\times$  ICP 7035. Indeterminate lines ICPL 143 and 161 were developed from crosses 'Pant A2'  $\times$  Baigani and Pant A2  $\times$  ICP 6, respectively. Prabhat, Pant A2, and UPAS 120 are short-duration cultivars and ICP 7035 is a long-duration landrace from Madhya Pradesh, India. Baigani and ICP 6 are medium-duration landraces from Andhra Pradesh and Madhya Pradesh, respectively. These lines were crossed in all possible combinations without reciprocals in the 1984 rainy season (July–November) at the ICRISAT Cooperative Research Center at Hisar, India. In the 1985 rainy season, half of the  $F_1$  seed was kept in cold storage and half was advanced under mosquito net cages to produce selfed  $F_2$  seed. The  $F_1$  plants were also crossed to each parent in 1985 to obtain reciprocal backcross seeds for each pair of parents.

In the 1986 rainy season, the parents,  $F_1$ ,  $F_2$  and reciprocal  $BC_1F_1$  of all 15 crosses were grown at Hisar. All populations were grown in 4-m long rows spaced 60 cm apart, with 15 cm between plants within rows. Parents and  $F_1$ 's were planted in single-row plots; backcross and  $F_2$  populations were planted in 2- and 20-row plots, respectively. At flowering the number of DT, SDT and IDT plants in each plot were recorded. Chi-square analysis was used to test the significance of deviation from expected segregation.

### RESULTS AND DISCUSSION

All six parents used in this study bred true for growth habit. The DT  $\times$  DT, SDT  $\times$  SDT and IDT  $\times$  IDT crosses showed no segregation in any generation, suggesting that two parents of a particular growth habit carried identical genes (Table 1).

#### Determinate $\times$ Semideterminate

All the  $F_1$  plants in the crosses involving DT  $\times$  SDT parents and  $BC_1F_1$  plants with the SDT parent ( $P_2$ ) were of SDT type for all four crosses (Table 2), indicating the dominance of the gene or genes governing

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SDT growth habit over those for DT growth habit. The  $F_2$  progeny of each cross showed a 3:1 segregation ratio of SDT and DT types (Table 2). The same segregation ratio was found in the pooled data of these four crosses (heterogeneity  $\chi^2$  was nonsignificant), indicating that the SDT character is controlled by a single dominant gene. In all four crosses, the  $BC_1F_1$  with DT ( $P_1$ ) parents segregated 1:1 SDT/DT, and with SDT ( $P_2$ ) parents produced only SDT plants. The pooled data also showed the same segregation as with individual backcrosses, confirming the control of SDT character by a single dominant gene.

### Determinate $\times$ Indeterminate Crosses

The data of pooled as well as individual crosses of  $F_1$  plants involving DT  $\times$  IDT parents (Table 3) showed that the gene or genes for IDT growth habit are dominant over those for DT growth habit. Reddy and Rao (1974), and Waldia and Singh (1987) also found the dominance of IDT growth habit over DT growth habit in pigeonpea. Bernard (1972) in soybean [*Glycine max* (L.) Merr.] and Brimo (1983) in broad bean (*Vicia faba* L.) also reported the dominance of IDT growth habit over DT growth habit.

The  $F_2$  segregation patterns and backcross data in pooled as well as in individual crosses between DT  $\times$  IDT parents (Table 3) agreed with the conclusion that

the IDT growth habit is governed by a single dominant gene. Reddy and Rao (1974) reported similar results; however, Waldia and Singh (1987) suggested involvement of two dominant genes, with inhibitory interaction of one of them to control the IDT growth habit.

Table 1. Number of individuals in different generations of pigeonpea crosses between parents of the same growth habit.<sup>†</sup>

Cross or generation	Observed segregation			Expected segregation
	IDT	SDT	DT	
<u>DT <math>\times</math> DT cross</u>				
ICPL 83008 ( $P_1$ ) $\times$ ICPL 83024 ( $P_2$ )				
$F_1$	—	—	22	All DT
$F_2$	—	—	549	All DT
$P_1 \times F_1$	—	—	80	All DT
$P_2 \times F_1$	—	—	19	All DT
<u>SDT <math>\times</math> SDT cross</u>				
ICPL 269 ( $P_1$ ) $\times$ ICPL 83032 ( $P_2$ )				
$F_1$	—	20	—	All SDT
$F_2$	—	58	—	All SDT
$P_1 \times F_1$	—	24	—	All SDT
$P_2 \times F_1$	—	29	—	All SDT
<u>IDT <math>\times</math> IDT cross</u>				
ICPL 143 ( $P_1$ ) $\times$ ICPL 161 ( $P_2$ )				
$F_1$	29	—	—	All IDT
$F_2$	198	—	—	All IDT
$P_1 \times F_1$	37	—	—	All IDT
$P_2 \times F_1$	33	—	—	All IDT

<sup>†</sup> DT = determinate, IDT = indeterminate, and SDT = semideterminate.

Table 2. Segregation pattern for growth habit<sup>†</sup> in pigeonpea crosses involving DT and SDT parents.

Cross or generation	Observed segregation			Expected segregation	$\chi^2$ value	Range of probability
	IDT	SDT	DT			
<u>DT <math>\times</math> SDT Crosses</u>						
ICPL 83008 ( $P_1$ ) $\times$ ICPL 269 ( $P_2$ )						
$F_1$	—	30	—	All SDT		
$F_2$	—	87	27	3:1	0.10	0.70–0.80
$P_1 \times F_1$	—	29	21	1:1	1.28	0.20–0.30
$P_2 \times F_1$	—	25	—	All SDT		
ICPL 83008 ( $P_1$ ) $\times$ ICPL 83032 ( $P_2$ )						
$F_1$	—	18	—	All SDT		
$F_2$	—	603	190	3:1	0.45	0.50–0.60
$P_1 \times F_1$	—	26	28	1:1	0.08	0.70–0.80
$P_2 \times F_1$	—	62	—	All SDT		
ICPL 83024 ( $P_1$ ) $\times$ ICPL 269 ( $P_2$ )						
$F_1$	—	20	—	All SDT		
$F_2$	—	473	160	3:1	0.03	0.80–0.90
$P_1 \times F_1$	—	37	38	1:1	0.02	0.80–0.90
$P_2 \times F_1$	—	72	—	All SDT		
ICPL 83024 ( $P_1$ ) $\times$ ICPL 83032 ( $P_2$ )						
$F_1$	—	20	—	All SDT		
$F_2$	—	586	212	3:1	1.04	0.30–0.40
$P_1 \times F_1$	—	31	35	1:1	0.24	0.60–0.70
$P_2 \times F_1$	—	27	—	All SDT		
Pooled (DT $\times$ SDT crosses)						
$F_1$	—	88	—	All SDT		
$F_2$	—	1749	589	3:1	0.05	0.80–0.90
$P_1 \times F_1$	—	123	122	1:1	0.01	0.90–0.95
$P_2 \times F_1$	—	186	—	All SDT		

<sup>†</sup> DT = determinate, IDT = indeterminate, and SDT = semideterminate.

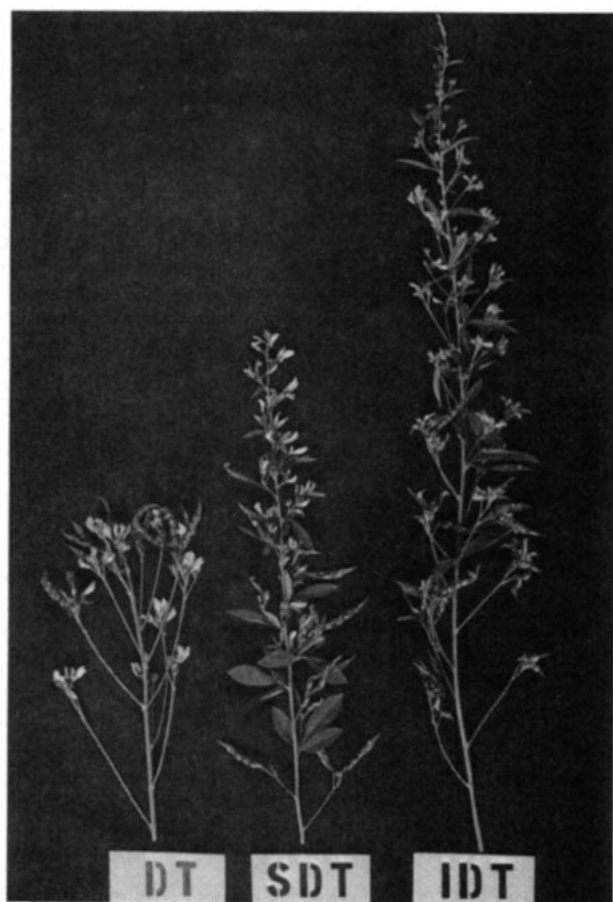


Fig. 1. Inflorescence showing growth habits in pigeonpea: determinate (left), semideterminate (center), and indeterminate (right).

Table 3. Segregation pattern for growth habit† in pigeonpea crosses involving DT and IDT parents.

Cross or generation	Observed segregation			Expected segregation	$\chi^2$ value	Range of probability
	IDT	SDT	DT			
<u>DT <math>\times</math> IDT crosses</u>						
ICPL 83008 ( $P_1$ ) $\times$ ICPL 143 ( $P_2$ )						
F <sub>1</sub>	30	—	—	All IDT		
F <sub>2</sub>	573	—	226	3:1	4.57	0.02–0.05
$P_1 \times F_1$	36	—	38	1:1	0.06	0.80–0.90
$P_2 \times F_1$	37	—	—	All IDT		
ICPL 83008 ( $P_1$ ) $\times$ ICPL 161 ( $P_2$ )						
F <sub>1</sub>	29	—	—	All IDT		
F <sub>2</sub>	139	—	35	3:1	2.21	0.10–0.20
$P_1 \times F_1$	21	—	25	1:1	0.34	0.50–0.60
$P_2 \times F_1$	78	—	—	All IDT		
ICPL 83024 ( $P_1$ ) $\times$ ICPL 143 ( $P_2$ )						
F <sub>1</sub>	20	—	—	All IDT		
F <sub>2</sub>	616	—	184	3:1	1.71	0.10–0.20
$P_1 \times F_1$	36	—	34	1:1	0.06	0.80–0.90
$P_2 \times F_1$	68	—	—	All IDT		
ICPL 83024 ( $P_1$ ) $\times$ ICPL 161 ( $P_2$ )						
F <sub>1</sub>	27	—	—	All IDT		
F <sub>2</sub>	607	—	188	3:1	0.77	0.40–0.50
$P_1 \times F_1$	18	—	16	1:1	0.12	0.70–0.80
$P_2 \times F_1$	39	—	—	All IDT		
Pooled (DT $\times$ IDT crosses)						
F <sub>1</sub>	106	—	—	All IDT		
F <sub>2</sub>	1935	—	633	3:1	0.17	0.60–0.70
$P_1 \times F_1$	111	—	113	1:1	0.02	0.80–0.90
$P_2 \times F_1$	222	—	—	All IDT		

† DT = determinate, IDT = indeterminate, and SDT = semideterminate.

## Semideterminate × Indeterminate Crosses

All plants in the F<sub>1</sub> generation of crosses between SDT × IDT parents were IDT. The F<sub>2</sub> population of each cross as well as pooled data gave a good fit to a dominant epistatic ratio for two loci of 12:3:1 IDT/SDT/DT (Table 4). This indicates that the SDT and IDT growth habits were governed by two nonallelic genes. The dominant gene controlling the IDT growth habit masked the expression of the other gene controlling the SDT growth habit. The backcross progeny of F<sub>1</sub> (IDT phenotype) with P<sub>1</sub> (SDT) parents segregated 1:1 IDT/SDT, but with P<sub>2</sub> (IDT) parents all progeny were IDT (Table 4). These observations further confirm the presence of two nonallelic genes with dominant epistatic action.

The results presented in Tables 1 through 4 indicate that the DT, SDT and IDT growth habits in the parents studied are governed by two epistatic genes. One of these, designated as *Dt<sub>1</sub>/dt<sub>1</sub>* conditions the IDT growth habit when *Dt<sub>1</sub>* is present (*Dt<sub>1</sub>\_\_\_Dt<sub>2s</sub>\_\_\_* or *Dt<sub>1</sub>\_\_\_dt<sub>2s</sub>dt<sub>2s</sub>*). The other gene, designated as *Dt<sub>2s</sub>/dt<sub>2s</sub>*, controls the SDT growth habit when *Dt<sub>2s</sub>* is present but only in the absence of *Dt<sub>1</sub>* gene (*dt<sub>1</sub>dt<sub>1</sub>Dt<sub>2s</sub>Dt<sub>2s</sub>* or *dt<sub>1</sub>dt<sub>1</sub>Dt<sub>2s</sub>\_\_\_*). The presence of *Dt<sub>1</sub>* allele completely masks the expression of *Dt<sub>2s</sub>* allele. The presence of the recessive alleles of these genes in homozygous state (*dt<sub>1</sub>dt<sub>1</sub>dt<sub>2s</sub>dt<sub>2s</sub>*) results in the DT growth habit.

Our results agree with the findings of Reddy and Rao (1974). Waldia and Singh (1987) reported two dominant genes, with the inhibitory interaction of one of them controlling the IDT growth habit. Their findings were based on the segregation pattern in two

Table 4. Segregation pattern for growth habit† in pigeonpea crosses involving SDT and IDT parents.

Cross or generation	Observed segregation			Expected segregation	$\chi^2$ value	Range of probability
	IDT	SDT	DT			
<u>SDT <math>\times</math> IDT crosses</u>						
ICPL 269 ( $P_1$ ) $\times$ ICPL 143 ( $P_2$ )						
F <sub>1</sub>	18	—	—	All IDT		
F <sub>2</sub>	217	54	21	12:3:1	0.46	0.70–0.80
P <sub>1</sub> $\times$ F <sub>1</sub>	10	12	—	1:1	0.18	0.60–0.70
P <sub>2</sub> $\times$ F <sub>1</sub>	43	—	—	All IDT		
ICPL 269 ( $P_1$ ) $\times$ ICPL 161 ( $P_2$ )						
F <sub>1</sub>	22	—	—	All IDT		
F <sub>2</sub>	349	103	35	12:3:1	2.93	0.20–0.30
P <sub>1</sub> $\times$ F <sub>1</sub>	27	29	—	1:1	0.08	0.70–0.80
P <sub>2</sub> $\times$ F <sub>1</sub>	40	—	—	All IDT		
ICPL 83032 ( $P_1$ ) $\times$ ICPL 143 ( $P_2$ )						
F <sub>1</sub>	22	—	—	All IDT		
F <sub>2</sub>	592	155	53	12:3:1	0.44	0.80–0.90
P <sub>1</sub> $\times$ F <sub>1</sub>	31	32	—	1:1	0.02	0.80–0.90
P <sub>2</sub> $\times$ F <sub>1</sub>	76	—	—	All IDT		
ICPL 83032 ( $P_1$ ) $\times$ ICPL 161 ( $P_2$ )						
F <sub>1</sub>	24	—	—	All IDT		
F <sub>2</sub>	584	173	43	12:3:1	4.93	0.05–0.10
P <sub>1</sub> $\times$ F <sub>1</sub>	34	38	—	1:1	0.22	0.60–0.70
P <sub>2</sub> $\times$ F <sub>1</sub>	58	—	—	All IDT		
Pooled (SDT $\times$ IDT crosses)						
F <sub>1</sub>	86	—	—	All IDT		
F <sub>2</sub>	1742	485	152	12:3:1	4.50	0.10–0.20
P <sub>1</sub> $\times$ F <sub>1</sub>	102	111	—	1:1	0.38	0.50–0.60
P <sub>2</sub> $\times$ F <sub>1</sub>	220	—	—	All IDT		

† DT = determinate, IDT = indeterminate, and SDT = semideterminate.

crosses involving DT × IDT parents. One explanation for the discrepancy between their results and ours is the effect of the date of sowing and spacing on phenotype observed. At Hisar, where Waldia and Singh conducted their study, if the seeds are sown in early June at a recommended spacing of 30 by 10 cm, the IDT plants usually attain a height of up to 3 m. This can suppress the growth of DT plants, particularly if they are surrounded by IDT-type plants. Hence, there is a possibility of missing some of the DT plants in the segregating populations, which could result in a different interpretation. Digenic inheritance of DT, SDT, and IDT growth habit has also been observed in soybean (Bernard, 1972); however, no epistasis was observed in that legume.

The information obtained here may be useful to pigeonpea breeders for developing promising high-yielding genotypes with desired growth habits. For high-input situations and mechanized cultivation, determinate pigeonpea cultivars have a production advantage due to their short stature and synchronous maturity, which makes them amenable to efficient crop management practices. On the other hand, for low-input situations where marginal farmers are not prepared to protect the crop from pest damage, the indeterminate growth habit may be advantageous.

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